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THE COLORS OF NORTHERN GAMOPETALOUS FLOWERS (*continued*).

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THE Lentibulariaceæ, or bladderwort family, are mostly aquatic or marsh plants. Only four genera and one hundred and eighty species are known. The flowers are yellow, or vary from yellow to purple and violet-blue. Of the fourteen species of Utricularia, or bladderwort, eleven species are yellow and three purple. The rootless plants of *Utricularia vulgaris* float near the surface during inflorescence. The deeply 2-lipped flowers are bright yellow with the palate marked with reddish-brown lines leading well down into the spur, which secretes the nectar. According to Knuth, Heinsius found the flowers visited only by long-tongued Syrphidæ, the species *Helophilus lineatus* being most numerous. This is certainly surprising as the closed flowers appear adapted to bees. As the species is aquatic considerable patience is required to observe the visitors. After repeated observations I have collected on the flowers in Maine only the syrphid fly *Helophilus conostomus*. Like Utricularia the genus Pinguicula is carnivorous, and the yellowish-green leaves are thickly covered with sticky glands. The flowers are violet-

blue with the palate covered with velvety white hairs. The visitors are flies and bees.

The Orobanchacæ are parasitic plants without chlorophyll, usually colored yellowish or purplish. The flowers also are frequently yellowish or purple. In variety luteum of *Aphyllon fasciculatum* the whole plant is yellow. Sometimes the flowers are bicolored, yellow or white, and purple.

The Bignoniaceae, or trumpet-creeper family, occur chiefly in the tropics. Many of the species are bird flowers, one to two inches in length, and crimson, orange or scarlet, as *Bignonia venusta* and *Tecoma radicans*. Common examples of bird flowers in North America are *Lobelia cardinalis*, *Gossypium herbaceum* and *Lonicera sempervirens*. The ruby-throated humming-bird, however, visits many flowers fertilized by insects. The Acanthaceæ, a large tropical family of some 1800 species, also contains many scarlet bird flowers.

The order Plantaginales includes but a single family, the Plantaginaceæ, or plantain family. The inflorescence is in spikes with small 4-merous flowers, which are mostly greenish or purplish, and are wind-fertilized. They are of special interest because they show the beginnings of adaptations to insect visitors. In one or more species, "we have before us the passage from anemophilous to entomophilous characters, the evolution of an entomophilous from an anemophilous species." *Plantago media* possesses a pleasant perfume and reddish filaments. Müller distinguishes an anemophilous and an entomophilous form, which differ slightly in color, the stamens, stigmas, and pollen. Twenty-four visitors have been collected on the flowers. The limb of the corolla and sometimes the border of the sepals of *P. alpina* is red. Five insects in the Alps have been collected on this species. According to Knuth, the flowers of Plantago display a variety of colors; in *P. major* the corolla is brownish, the filaments white, the anthers red, brown, or sometimes yellow or even white, while in other species yellow, red and violet appear.

The three orders, Rubiales, Valerianales, and Campanulales, which terminate the Gamopetalæ, exhibit many affinities with the families, which stand at the close of the Choripetalous

series. The individual flowers are usually small, and conspicuousness is gained by aggregation. The inflorescence is cymose forming in the Dipsaceæ and Compositæ dense involucrate heads, and not infrequently contracted in the other families belonging to this group into capitate clusters provided with an involucre, as in *Cephaëlis ipecacuana* of the Rubiaceæ. Both actinomorphic and zygomorphic flowers occur, and the sexes may be united or separated. By some writers the Rubiaceæ are derived from the Umbelliferæ. While this derivation is doubtful the terminal groups of the Choripetalæ and Gamopetalæ certainly possess many points of resemblance, which indicate a parallel development.

The Rubiales, which include the Rubiaceæ and Caprifoliaceæ, have opposite leaves, and usually the stipules are present in the first of the two families but rarely in the second. Stipules occur elsewhere in the Gamopetalæ only in the primitive stem family of the Loganiaceæ. The corolla varies greatly in length from rotate to funnelform and tubular, and is in consequence adapted to a great variety of visitors.

The Rubiaceæ, or madder family, is of immense extent in the tropics and contains about 5500 species. No other family contains so many dimorphous flowers. The roots of several species, as *Rubia tinctorum* and *Galium boreale* contain a red pigment (madder red), which is widely used in dyeing. The flowers of Galium, or bedstraw, are very small or minute, with the calyx obsolete. In *G. triflorum* and *G. circæzans* the flowers are green, in *G. boreale* and *G. mollugo* white, in *G. verum* yellow, in *G. rubrum* red, and in *G. purpureum* purple. The visitors are chiefly flies, and the great variety of colors affords evidence that they do not prefer one hue to another. Indeed the coloration of the different species is probably determined by internal conditions. *Houstonia cærulea*, or bluets, one of the common spring flowers, is pale blue or nearly white with a yellow eye. So abundant is this little plant that it often tinges the hillsides and meadows. Other species are blue or purple.

The Caprifoliaceæ, or honeysuckle family, are remarkable for the variation in length of the corolla tube, and the consequent adaptation of the flowers to a great variety of visitors. The

white, wheel-shaped flowers of Sambucus contain no honey, and are sparingly visited by flies and pollen-collecting bees. The large, pyramidal or flat cymes are very numerous and conspicuous. The small, rotate flowers of Viburnum are in large compound cymes, which bloom in early spring and midsummer. They are white, fragrant, and nectariferous. The most important visitors are Andrenidæ, flies and beetles, to which the inflorescence with its freely exposed honey is well adapted. I have found beetles more abundant and in greater variety than upon any other northern plants. The marginal flowers of *V. alnifolium* and *V. opulus* are sterile and greatly enlarged.

There are a few flowers adapted to wasps and to which these insects are very frequent visitors. The most important wasp flowers are *Epipactis latifolia*, *Cotoneaster vulgaris*, *Scrophularia nodosa*, *Symphoricarpos racemosa*, and *Lonicera alpigena*, the last two belonging to the Caprifoliaceæ. The flowers agree in having abundant honey secreted in a short corolla, or pouch-like receptacle, about the size of a wasp's head, and usually lurid colors. In England Darwin found *Epipactis latifolia* visited by swarms of wasps, but was astonished to observe that the sweet nectar never proved attractive to any kind of bee or dipterous insect. The small reddish flowers of *Symphoricarpos racemosus* (snow berry) are campanulate and pendulous. Wasps thrust their heads wholly into the flower to obtain the nectar. *Lonicera alpigena* is reddish-brown. Müller observed in the Alps that it was visited by two species of wasps in great numbers.

The nodding blossoms of *Linnæa borealis* are wine colored with a yellow marking on the lower side, which serves as a honey-guide, and exhale a sweet vanilla-like fragrance. It is a trailing evergreen vine densely carpeting the ground in cold, open woodlands. I have collected on the flowers only the fly *Empis rufescens*, which is rather common.

The large genus Lonicera is adapted to a variety of visitors. The wasp flower *L. alpigena* is reddish-brown. The bee flower *L. tartarica* is pink or white. The bumblebee flowers, *L. ciliata*, *L. xylosteum* and *L. cærulea* are yellow. The hawkmoth flower *L. periclymenum* on the first evening it expands is white within, changing to yellow on the second evening. The exterior of the

flowers is purplish-red, and in fading they turn to a dingy orange-brown. The bird flower *L. sempervirens* is scentless, scarlet outside and yellow within, or rarely throughout. The corolla of *Diervilla trifida*, or bush honeysuckle, is light yellow with an orange honey guide on the upper lobe. The older flowers turn reddish, a color change which also occurs in *Ribes aureum* and in the genera Weigelia, Fuchsia, and Lantana. In *Ribes aureum* Müller states that the more intelligent insects immediately recognize by means of their red color those flowers which no longer contain nectar, and consequently visit more blossoms in the same time. Repeated observations by the writer failed to show that the color change in Diervilla was of the same significance. The honeybee was observed to visit the red flowers both when solitary and when associated with yellow flowers. Neither was there any preference manifested for yellow flowers, when flowers of both colors occurred in the same cyme. An immense number of varieties of Weigelia have been produced in cultivation by selection and hybridization, which are remarkable for their wide range of coloring. There are white and deep red forms with every intermediate shade ; white when opening but changing to rose ; deep red in bud but rose-colored in bloom ; flowers pale rose at first, changing to deep red ; yellow ; light yellow, changing to white ; pale yellow, changing to pale rose ; and reddish-purple.

The herbaceous order Valerianales is intermediate between the Rubiales and the Campanulales. The flowers of the Valerianaceæ are in clustered cymes and are usually white or reddish. The inflorescence of the Dipsaceæ, or teasel family, is in involucrate, purplish heads, and is attractive to a great number and variety of insects. *Scabiosa atropurpurea* of the garden is black-purple, scarlet, or white. The distinct anthers and hanging ovule separate this family from the following order.

The Cucurbitaceæ, or gourd family, were formerly classed with the Choripetalæ, but are now placed in the order Campanulales with the Campanulaceæ and Compositæ. The species are herbaceous, tendril-bearing vines found chiefly in the tropics. The petals are separate or united. The smaller flowers of this family are white or greenish and the larger are yellow. The

pollinators are bees. "The flowers of a species of Trianosperma in South Brazil are visited, according to Fritz Müller, very abundantly all day long by *Apis mellifica* and a species of Melipona, although they are scentless, greenish, quite inconspicuous and to a great extent hidden by the leaves." In this instance as in some others the bees are probably guided by past experience in looking for the nectar. The large flowers of the cultivated Cucurbita are often wholly or partially concealed by the leaves, yet are readily found by bees.

The stem-family, or line from which the other families of this order are derived, is the Campanulaceæ, or bell-flower family. Of the twenty-three northern species one is red and twenty-two are blue. The flowers of Campanula are campanulate or rotate, blue or white, and are visited by many Hymenoptera. Lobelia has zygomorphic flowers which are usually blue or white. But *L. cardinalis*, *fugens*, *splendens* and *texenis*, have fiery red corollas adapted to humming-birds. There is no more brilliant red color in the northern flora than that of the corolla of *L. cardinalis*. Phyteuma and Jasione are transition genera.

At the head of the gamopetalous series stand the great family of the Compositæ, which includes such familiar and widely distributed plants as the thistle, aster, goldenrod, daisy and dandelion. About 1000 genera and 12,000 species have been described. Multitudes of these hardy weeds grow luxuriantly in our fields, and along our highways and hedgerows; and exhibit a remarkable vigor and ability to thrive under the most untoward conditions. Many of the species tend to become cosmopolitan, and have spread over both continents. The inflorescence represents Nature's greatest triumph in flower building. Intercrossing by insects, economy of time and material, a large number of seeds well adapted to germinate, and their wide distribution, have all been very perfectly attained. The individual flower is often very small, and of little significance as compared with the community. Conspicuousness is gained by massing a large number of flowers in a head, an arrangement that also permits insects to visit them very rapidly. In the goldenrod a head consists of ten or fifteen florets, while in the white weed the number may exceed five hundred. The capitulum with

its enfolding bracts often resembles a single flower, and was termed by the older botanists a compound flower. The life history of the individual florets may be conveniently studied in the garden sunflower, where they are of comparatively large size.

The Cichoriaceæ, or chicory family, are often treated as a tribe of the Compositæ. There are 8 white, 53 yellow, 5 red, 2 purple and 5 blue species. All of the flowers of the head are strap-shaped or ligulate, as in the dandelion. This species *Taraxacum taraxacum* (*T. officinale*) is gregarious, and in some localities the plants are so numerous that the inflorescence covers with a bright sheet of golden yellow entire hillsides. The visitors are numerous; in Low Germany Müller collected 67 Apidæ, 7 Lepidoptera, 25 Diptera and 16 other insects. Most of the genera of this family have yellow flowers as Hieracium (hawkweed), Latuca (lettuce) and Sonchus (sow thistle), but as a rule they are much less conspicuous than the dandelion and have fewer visitors. The great number of yellow flowers in this family have already been referred to under the Scrophulariaceæ. *Cichorium intybus* (chicory) has large bright blue flowers with white and pink variations.

The Ambrosiaceæ, or ragweed family, are composed of small greenish flowers, which in the absence of insects have reverted to wind-fertilization. In Ambrosia the corolla has been lost. At an earlier stage the flowers were homogamous or self-fertilized, as is still the case in *Senecio vulgaris* which is visited rarely by insects. The flowers excellently illustrate the fact that inconspicuousness is due to the absence of insects.

In the Compositæ the flowers are either tubular and all alike, when the head is called discoid; or the disk flowers are tubular and the marginal flowers are ligulate, when the head is radiate. There are 21 green, 126 white, 209 yellow, 4 red, 64 purple, and 59 blue flowers.[1] When the heads are discoid the flowers are all of the same color, but when they are radiate they are frequently bicolored. In the garden daisy, or *Bellis perennis*, the disk flowers are yellow, and the ray flowers are white, pink, or purple, with purple bracts. In Townsendia the disk flowers

[1] In classifying bicolored capitula preference is given to the color of the rays.

are yellow, and the ray flowers are white, violet, or purple. In Aster the rays are white, pink, purple, or blue, and the disk flowers are yellow turning to red-purple or brown. In the China asters (Callistephus) there is a great variety of colors, and a single head is often tricolored, as a yellow center surrounded by an inner white ring and an outer ring of purple. The ray flowers of this genus may display almost every imaginable shade of color, and individual flowers may change from white to rosy red or lilac. But in Helianthus and in part of the species of Coreopsis both ray and disk flowers are golden yellow. The original color of the genera, which was usually yellow, is preserved by the central or disk flowers. The rays may vary from yellow to white, red, purple or blue, and an innumerable number of intermediate shades. Under cultivation *Chrysanthemum sinense* has yielded a multitude of magnificent flowers. The ray flowers have increased in number until they compose the entire head, and there is scarce a tint or shade save blue that is not known. The original colors were a pale yellow, a white and a very weak violet shade, and from these have been raised all the colors and shades now seen in this flower. "This has been accomplished by a very slow and persistent selection and cross-fertilization. It is worthy of notice how intensified the yellows have become, and how many shades of this color there now are. The lilac has become pink of pure shading; then, as to red, *cullingfordii* often presents us with a pure tone of red. The most pronounced purple we have to-day is from the lightly tipped, incurved Princess of Wales, being a sport named Violet Tomlin. It is really purple. Now we cannot get purple without blue, and to those who are at work in this field of development, a blue chrysanthemum would not be such a great surprise." [1]

Throughout the Compositæ the corolla has remained of small size, and there is no reason to suppose it has ever been greatly modified in form. The primitive colors have also been very largely retained, for out of 483 northern species 209 are yellow and 126 white. Fifty of our genera contain yellow flowers, and some large genera consist wholly of flowers of this color,

[1] Thorpe, J. *Amer. Garden*, vol. xi, No. 1, p. 4.

as Chrysopsis, or golden aster, Solidago (with one exception), and Senecio. The capitula are both discoid and radiate, and as a rule both ray and disk flowers are yellow. But the disk flowers in some genera have become brown or purple. In Rudbeckia, or cone flower, the rays are yellow and the disk purple; in Helianthus six species have the disk purple or brown, and in sixteen species the disk is yellow; and in Coreopsis both rays and disk vary from yellow to brown.

One hundred and twenty-six species have white flowers. In many instances where the ray flowers are white the disk flowers are yellow. In these bicolored capitula there can be little doubt that the white rays are derived from yellow-flowered progenitors. In Verbesina (crownsbeard) all of the five species have yellow disks, but one has white and four yellow rays. The white discoid heads seem also to have been originally yellow. Of the discoid heads of Hymenoppapus two species are yellow and three are white. A number of genera, as Antennaria, Filago and Gnaphalium, consist of white woolly herbs with yellowish white often inconspicuous flowers, which have undergone much retrogression. The white-flowered species appear to be of later origin than the yellow, and in numerous instances to be derived from them.

There are only four red to sixty-four purple, and fifty-nine blue flowers. The heads are both discoid and radiate. While the rays may change directly from yellow to red, purple, or blue, in many instances they have probably passed through an intermediate white stage. In Boltonia, which has the disk yellow, one species has the rays white, and in two others they are blue or violet. In Aster the rays are white in twenty-two species, purple in six, and blue in forty-four. In Erigeron the white rayed species frequently vary to pink or purple. In Coreopsis twelve species have the rays yellow like the disk, but in one they are pink, and in the variety Golden Wave they often change from golden yellow to maroon. In some species of Aster the disk flowers change from yellow to red or blue, as in *A. roscidus*, *A. carmesinus*, and in *A. curvescens*. Whether the purple discoid flowers of Vernonia (iron-weed) have passed through a yellow stage there is little evidence. The flowers of Artemisia (worm-

wood) have reverted to wind-fertilization and are greenish or yellowish.

The individual flower in the Compositæ is small and of little significance. Conspicuousness is gained by massing first the flowers, then the capitula, and finally the plants themselves. If the capitulum is large, as in Helianthus, it may be solitary, but if small, as in Solidago, they may be aggregated into dense flower-clusters. Many species are, moreover, gregarious, and so abundant that they constitute important features in the floral landscape. Such are the white weed, thistle, sunflower, goldenrod, and aster. Kerner states that in New Zealand the small white flowers of Haastia are so densely aggregated that they form hemispherical mounds two feet high by three feet in length. The plant is known as "vegetable sheep" since at a distance it is frequently mistaken for that animal.

With the exception of the Umbelliferæ, or carrot family, no flowers are visited by so large and miscellaneous a company of insects as the Compositæ. The guests of a single species may exceed one hundred in number. The nectar is more deeply concealed than in the Umbelliferæ, and the percentage of long-tongued visitors is consequently much greater. Throughout the Compositæ bright coloration is correlated with pollination by insects; and when a genus reverts to wind-fertilization, the inflorescence becomes inconspicuous. It is interesting to note that the species, which attract the largest number of visitors, display a variety of colors, as in the bright yellow goldenrods, *Chrysanthemum leucanthemum* with white rays and a yellow disk, *Achillea millefolium* white or tinged with red, the asters with a yellow disk and white or blue rays, and the purple-flowered Canada thistle. These differently colored species are visited by a large company of Hymenoptera, Lepidoptera, Diptera and Coleoptera, which are influenced by the length of the corolla tube and the degree of conspicuousness obtained by a contrast of colors and by massing; but there does not seem to be any evidence that they find greater pleasure in one hue than in another. The white-flowered *Eupatorium perfoliatum* (thoroughwort) in this locality is visited by a larger number of butterflies than any other Composite plant. Bumblebees are also very common and

as pollinators far more important than the butterflies. No one, however, would claim that the color of this species was due to the selective influence of either bees or butterflies. In a woodland pasture I found two large patches of the common elecampane, or *Inula helenium*, and the Canada thistle growing side by side. The yellowish-red butterfly, *Argynnis aphrodite* was flitting about upon the large yellow flowers of Inula, for which it showed a decided preference, though occasionally it was observed to fly over to the purple flowers of the thistle. The white cabbage butterfly on the contrary confined its visits almost exclusively to the thistle blooms. As red has been supposed to be the favorite color of butterflies, this singular behavior must have been determined by other causes than the colors of the flowers. *Argynnis aphrodite* also very frequently visits the small white flowers of *Aralia hispida*, and *Pieris rapæ* delights in the white or reddish flowers of the garden radish.

Bees not infrequently pass from one species to another in this family, both when the flowers are closely allied and when they are widely different. I have often seen bumblebees pass from one species of goldenrod to another, and even back and forth between goldenrods and asters. Occasionally I have seen them pass between very different forms of flowers, as between sunflowers and the scarlet runner, or the goldenrod and the purple vervain (*Verbena hastata*). On the other hand the honeybee often displays a remarkable power of distinguishing between closely allied species, even when they are of the same color. One of the common golden-rods *Solidago lanceolata* has its capitula arranged in a crowded, flat-topped corymb. Another common variety *S. rugosa* has the inflorescence panicled. In an upland pasture these two species were found growing together, the panicled form being much the more abundant. Honeybees, the only insects present, showed a marked preference for *S. lanceolata*, though they occasionally passed over to the other species. They were repeatedly seen to leave *S. lanceolata*, and after flying about but not resting on the flowers of *S. rugosa* return to the plants they had left only a few moments before. In another instance a bee was seen to wind its way among the plants of the latter species until it found an isolated plant of *S. lanceolata*.

A plant of each of the above species was bent over so that the blossoms were intermingled, appearing as a single cluster; a honeybee rested on *S. lanceolata*, and it seemed very probable that it would pass over to the flowers of *S. rugosa*, but such was not the case, for presently it flew away to another plant of the former. The behavior of these bees in their endeavors to adhere to a single species was thus attended both by loss of time and repeated visits to the same blossoms. On another occasion the whitish or cream-colored inflorescence of *Solidago bicolor* was observed to be very frequently visited by the males of *Bombus bifarius*, while the yellow-flowered goldenrods in the vicinity were entirely neglected. By holding yellow-flowered clusters directly in their way, I repeatedly induced these bees to leave *S. bicolor*; but they quickly perceived that they had passed to a different flower, and invariably after a few seconds or sometimes instantly returned to the cream-colored species. They were probably influenced by the greater supply of nectar in the flowers of *S. bicolor*. The plants, which were growing on burnt land, were of unusually large size, and secreted nectar very freely as I ascertained by examination on my return home. These illustrations are sufficient to show that the influence of particular colors in determining the visits of insects may be easily overestimated.

THE COLORS OF NORTHERN GAMOPETALOUS FLOWERS.

Orders.	Families.	Green.	White.	Yellow.	Red.	Purple.	Blue.	Total.
Ericales	Clethraceæ		2					2
	Pyrolaceæ	1	7		2	1		11
	Monotropaceæ		3		1			4
	Ericaceæ		22	1	10	5		38
	Vacciniaceæ	2	10		11			23
	Diapensiaceæ		3					3
Primulales	Primulaceæ		4	11	7			22
	Plumbaginaceæ				1	1		2
Ebenales	Sapotaceæ		2					2
	Ebenaceæ			1				1
	Symplocaceæ			1				1
	Styraceæ		4					4
Gentianales	Oleaceæ	7	2			1		10
	Loganiaceæ		2	1	1			4
	Gentianaceæ		7	1	10	4	16	38
	Menyanthaceæ		2	2				4
	Apocynaceæ		2	1	1	1	2	7
	Asclepiadaceæ	7	11	3	5	13		39
Polemoniales	Convolvulaceæ		7	1	7		3	18
	Cuscutaceæ		11		1			12
	Polemoniaceæ		7		10	3	8	28
	Hydrophyllaceæ		8				10	18
	Boraginaceæ		19	6		1	17	43
	Verbenaceæ		2			2	8	12
	Labiatæ		24	4	12	47	33	120
	Solanaceæ		9	21		2	8	40
	Scrophulariaceæ		13	33	7	32	28	113
	Lentibulariaceæ			11		3	2	16
	Orobanchaceæ		1	2		2	2	7
	Bignoniaceæ		2	1	1			4
	Martyniaceæ		1					1
	Acanthaceæ				1	1	5	7
	Phrymaceæ					1		1
Plantaginales	Plantaginaceæ	14	1					15
Rubiales	Rubiaceæ	4	22	1		7	5	39
	Caprifoliaceæ		22	11	4	1		38
	Adoxaceæ	1						1
Valerianales	Valerianaceæ		5		4		1	10
	Dipsaceæ					4		4
Campanulales	Cucurbitaceæ		4	1				5
	Campanulaceæ				1		22	23
	Cichoriaceæ		8	53	5	2	5	73
	Ambrosiaceæ	15						15
	Compositæ	21	126	209	4	64	59	483
	Total	72	375	376	106	198	234	1361

SUMMARY AND CONCLUSIONS.

Numerical Summary.—In the territory extending northward from the parallel of the northern boundary of North Carolina and Tennessee to the northern limits of Labrador and Manitoba, and from the Atlantic Ocean westward to the 102d meridian, there are recognized in the Illustrated Flora of Britton and Brown 4020 angiospermous plants. In the following table the species belonging to the different series have been arranged according to their predominant floral colors.

Series.	Green.	White.	Yellow.	Red.	Purple.	Blue.	Total.
Monocotyledons	857	82	41	22	22	34	1058
Dicotyledons							
Choripetalæ							
Apetalæ . .	175	89	51	45	24		384
Polypetalæ .	140	410	333	84	193	57	1217
Gamopetalæ .	72	375	376	106	198	234	1361
Total . .	1244	956	801	257	437	325	4020

In every 100 species there are 30.9 green, 23.8 white, 19.9 yellow, 06.4 red, 10.9 purple and 08. blue. The hydrophilous and anemophilous species within this area, I place at about 1048, of which 1021 are green, 1 white, 11 yellow, 3 red and 12 purple. A number of species vary between wind-fertilization and insect-fertilization, and are differently classed by different observers. *Empetrum nigrum* according to Warming is a wind-flower, according to Lindman an insect flower, and according to Knuth it is a wind-flower with occasional insect visits. There are then in the district under consideration 2972 species, which are fertilized by insects or are self-fertilized. Of this number 223 are green, 955 white, 790 yellow, 254 red, 425 purple, and 325 blue. In every 100 of these plants 07.5 are green, 32.1 white, 26.6 yellow, 08.5 red, 14.3 purple, and 10.9 blue. It is evident that anemophily and small greenish flowers are correlated, and that large bright colored flowers are due to insect fertilization. The 1048 Anemophilæ and Hydrophilæ are dis-

tributed as follows: — Monocotyledones 802 green; Apetalæ 134 green, 1 white, 11 yellow, 2 red, and 4 purple; Polypetalæ 27 green, 1 red, and 8 purple; Gamopetalæ 58 green species.

The Pigments. — The colors of angiospermous plants are due to three groups of pigments, occurring either singly or associated together; the green pigments or chlorophyll; the yellow pigments which include carotin, xanthophyll and phyllofuscin; and the soluble red and blue pigments or anthocyan.

Chlorophyll. — The characteristic green shades of foliage are caused by chlorophyll, the most common of all plant pigments. With the exception of the Fungi it is found in nearly all forms of vegetation, though its presence is often partially masqued, as in the Algae, by its association with other coloring substances. Its wide distribution is explained by its activity in the synthesis of carbohydrates. According to several late investigators there is more than one kind of chlorophyll. This view was adopted in 1895 by Gautier and Etard. Kohl in his recent work on "Carotin" admits of two varieties, which he designates as α-chlorophyll and β-chlorophyll.[1] In a green leaf "the normal chloroplasts contain much α-chlorophyll, little β-chlorophyll, much carotin, little α-xanthophyll, and little β-xanthophyll." [2] The α-chlorophyll is to be regarded as pure chlorophyll. Its absorption bands lie in the red half of the spectrum. The genetic relations of chlorophyll require further investigation. Wiesner's theory that etiolin is the mother substance of chlorophyll has not been proven; and, according to Kohl, it can be shown that in the greening of etiolated plants chlorophyll is not formed at the expense of the etiolin. The different shades of green observable in foliage are due partly to the quantity and arrangement of the chloroplasts. The upper side of a leaf is usually a darker green than the lower, because the palisade cells contain three or four times as many chlorophyll granules as the spongy parenchyma of the lower side.[3] Ferns and mosses, which habitually live in shady ravines, are a deeper green in

[1] Kohl, F. G. *Untersuchungen über das Carotin und seine physiologische Bedeutung in der Pflanze*, p. 139.

[2] Ibid. p. 145.

[3] Kerner. *Natural History of Plants*, vol. i, p. 374.

such locations than when they grow in the open sunlight. The color is also affected by a change in the position of the granules under the action of intense light, as may be observed in *Lemna trisulca* and many seaweeds.[1] Chlorophyll is readily soluble in alcohol yielding a green solution, which is soon destroyed in direct sunlight. There is a constant destruction and renewal of chlorophyll in living leaves under the action of bright light, so that on the same plant the leaves present different shades of green. Green seaweeds, when left on the beach by the waves, soon turn yellowish owing to the destruction of the chlorophyll.

Leaves and flowers may in some instances owe their particular shade of color to the presence of chlorophyll mixed with some other pigment. The dull purple of *Scopolia atroipoides* and *Atropa belladonna*, according to Hildebrand, are caused by green grains mingled with violet-colored sap. In the gooseberry, says Möbius, the brownish color of the flower is due to an upper layer of cells containing red cell sap, and an under layer containing chlorophyll. Many greenish yellow and purple flowers appear to contain chlorophyll. The tints of autumn leaves are also modified by its presence in greater or less quantities, while in normal green leaves it is often accompanied by anthocyan.

Yellow Pigments.—Chlorophyll is invariably accompanied in the chloroplasts by carotin, the yellow pigment so common in the root of the carrot. Tammes[2] and Kohl[3] found carotin to be widely distributed in the blue, green, red, and brown Algæ; in the Fungi, lichens, mosses, and ferns; in green, yellow, etiolated and autumn leaves; and in flowers, fruits and seeds. There is, however, no evidence of any genetic relation between the two pigments; and carotin may exist independently in organisms in which chlorophyll does not occur, as in Bacteria, fungi, the root of *Daucus carota* and in yellow flowers and leaves. Kohl finds that etiolin is identical with carotin, and adds that the term etiolin in the sense used by Pringsheim

[1] Sach. *Physiology of Plants*, p. 618.

[2] Tammes, Tine. Ueber die Verbreitung des Carotins in Pflanzenreiche. *Flora od. Allg. bot. Zeitung*. Bd. 87, H. 2, p. 244.

[3] The distribution and properties of the yellow pigments are discussed at length in Kohl's exhaustive work on Carotin.

should be stricken from the list of plant pigments. Etiolated plant organs owe their coloring exclusively to carotin, with which is often associated anthocyan. Also identical with carotin are xanthopyll and anthoxanthin as these terms are commonly used. Carotin ($C_{26} H_{38}$) is easily dissolved by ether but is insoluble in water. The melting point is 167.8C. Concentrated sulphuric and nitric acid color it a dark blue. Its crystals are rhombic. The functions of carotin, according to Kohl, are threefold. First it aids in assimilation. Its absorption bands lie in the blue half of the spectrum, and, together with those of chlorophyll, give the absorption spectra of the crude leaf-green. "Both take an important, though unlike part, in the assimilatory work of the chloroplasts, both absorb supplementarily to each other a part of the sunlight and assist in the decomposition of the atmospheric carbonic acid." Secondly, carotin may serve as a reserve product, as in a number of Fungi and Algæ and in the root of *Daucus carota*. Thirdly, it is of biological importance because it renders flowers, fruits and seeds conspicuous and attractive to insects and birds, which aid in their fertilization and dissemination. Among the flowers which owe their yellow color to carotin are, *Abutilon nervosum*, *Adonis vernalis*, *Cucurbita pepo*, *Eranthis hyemalis*, *Forsythia viridissima*, *Geum montanum*, *Helianthus annuus*, *Impatiens noli-tangere*, *Kerria japonica*, *Œnothera biennis*, yellow flowered roses, *Taraxacum officinale*, and *Tropæolum majus*.

In the peel or pericarp of the lemon, in the flowers of the yellow dahlia, in *Linaria vulgaris*, *Corydalis lutea*, the yellow parts of *Antirrhinum majus*, and in all the yellow flowering thistles, as well as in other flowers, the yellow pigment does not occur in plastids, but dissolved in the cell sap. What is this pigment? In a solution of crude leaf-green, in addition to carotin, there are two other yellow pigments, one of which was obtained by Tschirch in 1896 and the other by Schunck in 1899. Kohl proposes to designate the latter of these two pigments as α-xanthophyll and the former as β-xanthophyll. They differ both in their absorption spectra and chemical reactions. The α-xanthophyll occurs in small quantities in normal chloroplasts and yellow autumn leaves. It is the β-xanthophyll which colors the peel of the lemon and the flowers with yellow cell

sap. Both carotin and β-xanthophyll occur in species of Ranunculus, Verbascum, *Caltha palustris* and *Ribes aureum*. The β-xanthophyll can be obtained in a yellow solution by boiling in water the peel of the lemon. It becomes brown-colored with sulphuric acid and with ammonia a deeper yellow. This pigment was first isolated from the flowers of the dahlia nearly half a century ago.

In the chloroplasts of golden yellow-leaved plants, as Sambucus and Evonymus, Kohl finds yet another yellow pigment largely soluble in water to which he gives the name of phyllofuscin. In addition to this pigment he finds in yellow leaves much carotin, and more or less β-xanthophyll, but no α-xanthophyll or chlorophyll. Though they contain no chlorophyll such plants grow and perform the work of assimilation, in which process the chief part must be ascribed to carotin. Finally in yellow autumn leaves there is little or no chlorophyll, about the same amount of carotin as in the green leaf, little α-xanthophyll and much β-xanthophyll.

The yellow plastids of flowers are usually round and small, though sometimes angular as Tropæolum. Several other modifications also occur. In the tomato, asparagus, *Cratægus coccinea*, and in some species of Rosa and Physalis the plastids of the fruit are spindle-formed or irregularly shaped, and are fire-red, orange-red, or yellowish red. Tammes found that the red plastids of the tomato gave the usual reaction for carotin. In yellow leaves the plastids are round, but in autumnal yellow leaves they occur in irregular masses. The scarlet poppy, tulip and fire red canna owe their colors to a mixture of yellow plastids and red cell sap. On the other hand dingy or dull colors result from a combination of violet sap with yellow granules.

Anthocyan.—The red and blue colors of leaves, fruits and flowers are produced by a soluble pigment termed anthocyan. The ecological significance of this coloring substance, which is widely distributed in plants, is important and deserves further study. It is of frequent occurrence on the stems, veins and leaves of herbaceous plants, as well as on the under side of aquatic leaves and of radical leaves growing in rosettes, as in the Cruciferæ. In early spring, in autumn, and at high ele-

vation, it is particularly abundant. It probably serves to convert light rays into heat, and at the same time protects and aids in the translocation of the food materials. As in the previous instances we have undoubtedly to deal with a group of pigments. The formation of anthocyan has been studied by Overton with the aid of cultures of aquatic and land plants. Experiments with water cultures of Hydrocharis showed that light intensity and low temperature were favorable to the development of red cell sap. Plants of Hydrocharis were placed in a 2% solution of invert sugar, and also in pure water. The conditions of light and temperature were such that the water culture plants showed no change in color, while in a few days the plants in the invert sugar solution developed dark red coloring, especially in the new leaves. Experiments with other aquatic plants gave similar results. The red cell sap was contained chiefly in the palisade cells, though extending also to other cells of the mesophyll. Cut stems of *Lilium martagon* and other land plants placed in a 2% invert sugar solution soon developed red color in the palisade cells. The leaves of the control plants remained a pure green. As the result of many observations Overton concludes that a cell sap rich in sugar, low temperature, and intense light are connected with the production of red color. During the summer in the Alps the leaves of plants are much oftener red-colored than in the lowlands, because the night temperature is lower and the light intensity higher. Winter leaves become red-colored since the lower temperature causes the sugar content of the leaves to increase at the cost of the starch. In the ripening of red and violet-colored fruits the appearance of the coloring is also attended by the conversion of the starch into sugar. A few experiments were made to determine whether white flowering varieties of certain plants could artificially be caused to vary into red flowering varieties, but with negative results. In the case, however, of the greater intensity of color in Alpine flowers, and of white lowland flowers which become red-colored in the Alps, and also of flowers which are brighter colored in early spring than later in the season, it is probable that the lower temperature causes the conversion of starch into sugar.

The red pigment is probably a glucoside, or a very closely related compound, of which the constituents are a sugar and a tannic acid. Since in many plants, the provision of the cells with sugar increases the tendency to form red cell sap, there can be little doubt that a sugar forms part of the raw material out of which the pigment is built up. Tannins are also contained in the cells in which the red color has been formed by the artificial increase of sugar. The red color stuff is thrown down by the tannin reagents coffein and antipyrin, and the precipitate closely resembles those of the tannins. The behavior of the red pigment indicates that it is a tannin compound. The supposition that tannin is connected with the formation of the red and blue pigments of flowers is not new, but was first suggested by Wigand in 1862. It was observed that red color was formed only in cells that contained tannin. "If we examine," says Overton, "the reaction of the red color stuff upon different bases we obtain support for the opinion, that this pigment represents a weak bivalent or multivalent acid. For we find that its tinge is almost unnoticeably changed by very weak bases as coffein, antipyrin, etc., that with stronger bases, however, the color turns first into violet and blue, and with a greater excess of a strong base it finally changes into green. The most simple explanation of these phenomena is that the free acid is only little dissociated electrolytically and that the red color is peculiar to the molecules of the acid that has not been dissociated, the blue color would belong to the univalent, and the green color to the bivalent ions of the acid. On account of the weakness of the acid the bivalent ions would be found — in consequence of hydrolytic dissociation — in larger quantities only when a certain excess of a base is present." The capability of forming red cell sap appears to belong chiefly to the phanerogams, for the red color of mosses is confined to the cell membrane.[1] Many of the pigments found in plants and used for coloring are glucosides. The indigo blue of commerce is derived from the glucoside indican, which occurs in the plants of the leguminous genus Indigofera. Indigo red is also obtained from this gluco-

[1] Overton, E. Beobachtungen und Versuche über das Auftreten von rothem Zellsaft bei Pflanzen. *Jahrb. wissensch. Botanik*, Bd. xxxiii, H. 2.

side. From indigo may readily be obtained aniline remarkable for the great variety of dyes which it yields.

In darkness flowers differ greatly in the extent to which they develop their colors. *Silene pendulata* fails to show red coloring and *Prunella grandiflora* instead of developing dark violet color remains a pure white; while *Tulipa gesneriana* forms its red color and *Crocus vernus* its blue violet as perfectly in darkness as in light. The explanation given by Sachs, where bulbous plants produce normal flowers in darkness, is that the flower forming substance was already collected in the bulb, and had been stored up in a preceding period of vegetation in bright sunlight. Leaves, flowers and fruits often display red coloration only on the side exposed to direct sunlight. Kerner found that the anthocyan in plants grown in an Alpine garden at an elevation of 2195 metres above the level of the sea was brighter colored and more abundant than in the botanical garden at Vienna. At a high elevation the glumes of grasses, the leaves of stonecrops, and the pure white petals of some flowers become red or purplish-red.

When a red flower or a solution of red cell sap is treated with an alkali it changes to blue, but the red color is again restored by an acid. Red color is more common in foliage (where it is termed erythrophyll) than blue because an acid condition usually prevails in the leaf cells. In the Boraginaceæ with a decrease in the acidity of the cell sap the flowers change from red to blue; while an increase in the acidity of the cell sap will cause a normally blue flower to vary into a pink variety. "In some rare instances the blue pigment occurs in a solid form in flowers and also in fruit." In the fruit of the nightshade *Solanum americanum* the coloration is due to intense violet-colored crystalloids of rhombic form or in thin six-sided plates.[1] Blue grained pigments also occur in *Strelitzia regina*, *Tillandsia amœna*, and in *Delphinium elatum*.[2] The occurrence of blue pigment in solid form is probably to be explained by the evaporation of the free water. It never occurs in chromoplasts. Cells containing red and blue sap may occur indiscriminately

[1] Möbius, M. *Die Farben in der Pflanzenwelt*, p. 15.

[2] Hildebrand, Friedrich. *Die Farben der Blüthen*, p. 45.

near each other in the same flower, or the epidermis may contain blue cells beneath which in the mesophyll is a layer of red cells, as in *Viola odorata*.[1] Yellow chromoplasts and anthocyan occurring together give scarlet hues. The shades of flowers depend upon the density of the chromoplasts, and the number of layers of pigment cells, and the character of the epidermis.

Green Flowers.— Of the 223 green flowers classed as entomophilous many have no petals, as fifteen species of the Polygonaceæ and eight species belonging to the Caryophyllaceæ, also in several Rosaceæ, in *Acer saccharinum* and *Didiplis diandra*. Many are self-fertilized, as Triglochin and Scheuchzeria, and the orchids *Habenarea hyberborea* and *Epipactis viridiflora*, and the small green flowers of Lechea and *Penthorum sedoides*. Some have the petals caduceous and depend upon their scent to attract insects, as the Vitaceæ. Many are visited by flies and the smaller bees, as various Melanthaceæ, the Smilaceæ, the Anacardiaceæ, and the green flowers of the Asclepiadaceæ. But the green flowers of Asparagus are visited by the honeybee. As a whole, green flowers are small or even minute and attract few insects. A transition stage is represented by the genus Ribes, which contains species with greenish, white, reddish, and yellow flowers. As is well known many flowers pass through a green stage before their bright colors appear. Large green flowers, which are chiefly fragrant and nocturnal, are found in exotic Solanaceæ. Other examples are exhibited by the orchids, as several Brazilian species of Epidendrum. Green flowers, except in some cases of retrogression, belong to an early stage of development and their coloring requires no special explanation. The petals are modified leaves, and their primitive color is green similar to that of foliage. The larger green flowers may be explained by the greater persistency of the chlorophyll, for some species hold their colors much more strongly than others.

Yellow Flowers.—The development of bright coloration in flowers is an acquired habit. This is well illustrated by the sepals of *Helleborus niger*, which at first are large and white, but after fertilization develop chlorophyll, become a fresh green color and

[1] Möbius, M. *Die Farben in der Pflanzenwelt*, p. 3.

act as leaves. A similar change has been observed in many orchids and liliaceous plants. Virescence, or the occurrence of green flowers instead of those of the normal color, has been observed in many Ranunculaceæ, Umbelliferæ and Compositæ.[1] The formation of chlorophyll has but to cease, and under the action of light the petals will quickly lose their green color, with the result that in most instances the flower will change to yellow or white. If the yellow pigments, which are invariably associated, as has been shown, with the chlorophyll in the chloroplasts are persistent and continue to increase, the color of the flower will be yellow. The quantity of yellow pigments, it will be remembered, varies greatly in different plants. In some they are scarcely perceptible, in others they are so abundant as to tinge the whole plant yellow, while in a few golden yellow species they exclude all other pigments even the chlorophyll. If, however, the yellow color also vanishes we have a white flower. As would be expected yellow and white flowers are the most common, and are the earliest of the floral colors in their origin. A large number of yellow and white flowers with a mostly small, regular and primitive perianth occur in widely separated families.

Families.	Yellow.	White.	Green.	Red.	Purple.	Blue.	Total.
Melanthaceæ . .	7	10	5		2		24
Liliaceæ	6	13	1	11	1	6	38
Polygonaceæ . .	5	22	33	11	3		74
Ranunculaceæ . .	38	26	6	3	13	11	97
Cruciferæ . . .	46	54	2	1	10		113
Saxifragaceæ . .	6	30	4		3		43
Rosaceæ	39	35	4	13	4		95
Onagraceæ . . .	24	14	3	10	6		57
Umbelliferæ . .	16	58			1	3	78
Primulaceæ . . .	11	4		7			22
Solanaceæ . . .	21	9			2	8	40
Cichoriaceæ . . .	53	8		5	2	5	73
Compositæ . . .	209	126	21	4	64	59	483
Total . . .	481	409	79	65	111	92	1237

Many species of Compositæ, it will be noted, retain their primitive colors. In a few families white flowers occur unaccom-

[1] Masters, M. T. *Vegetable Teratology*, p. 339.

panied by yellow. In the aquatic Alismaceæ the entire nineteen species are white, and in the Caryophyllaceæ there are fifty-six white flowers but no indigenous yellow species. The six species of the Xyridaceæ on the other hand all produce yellow flowers. In the anemophilous Betulaceæ there are eleven yellow species, but flowers with a yellow calyx are rare in the Apetalæ. The Hypericaceæ are nearly monochromatic as twenty-two species are yellow and only two red. The zygomorphic Orchidaceæ contain ten yellow-flowered species, a larger number than any other monocotyledonous family. A surprisingly large number of yellow flowers occur in the zygomorphic Papilionaceæ (33 species), the Scrophulariaceæ (33 species), and the Lentibulariaceæ (11 species). This fact Müller attributes, and we think rightly, to the persistence of the primitive yellow in certain genera, and its little tendency to variation with the specialization of the flowers. In many families of the Gamopetalæ yellow flowers are absent, or are represented only by a single species, as in the orders Ericales, Ebenales, and Gentianales, where the inflorescence is chiefly white or red.

White Flowers.— White flowers are most abundant in the American as well as in the European flora. A white inflorescence is evidently a less tax on the energies of a plant than one containing pigments; and trees and shrubs, which produce their flowers in almost boundless profusion, as the Pomaceæ, Drupaceæ, Ilicaceæ, and the genus Viburnum, have almost exclusively white blossoms. In the writer's opinion white flowers are primarily due to degeneration. In this connection the studies of white leaves by Rodrique, Laurent and Timpe, which clearly show evidences of degeneration, are of interest. According to their investigations such leaves are thinner than normal green leaves, and consist wholly of cellular tissue with the palisade cells absent. It is desirable to consider very briefly some of the conditions under which white flowers occur, and under which they develop chromatism. They are derived both from primitively green and from high colored flowers. Small, densely clustered white flowers are common in the Cruciferæ, Saxifragaceæ, Umbelliferæ, Cornaceæ and Ericaceæ. In these flowers the stimulus to produce pigments is wanting and the leaf-green

colors, as may be observed in the Cornaceæ, fade away leaving the petals white. A check in nutrition and growth will cause bright colored flowers to become smaller and revert to white. This may be caused by cultivation in an impoverished soil, by transplanting, or by low temperature. In springtime white flowers are noticeably common. In the Baltic flora the graphic curve of white reaches its highest point in May, from which it gradually sinks to its lowest point in late autumn. In the arctic climate of Spitzbergen the flowers are chiefly white, and there are few yellow and red, while blue appears to fail entirely. In East Greenland the flowers are likewise chiefly white, and among twenty-six species there is only one blue.[1] Self-fertilization also causes a diminution of the corolla in size and a paleness or loss of color.[2] Bright colored flowers fertilized artificially with their own pollen in a few generations become paler; while white flowers, as would be expected, and what is more surprising white varieties of colored flowers adapted to insect-fertilization, are both usually self-fertilizing. They may also exhibit evidences of deterioration in their structure, as in Lepidium, Stellaria, and Sagina, where the petals are usually present but sometimes are wanting. In all of the instances cited there is a lack of vitality in the corolla due to insufficient nutriment. Let the growth of the plant now receive a stimulus and an increased brilliancy of the flowers soon makes itself apparent, as when they are exposed to clear sunlight or treated with nitrate of soda, and may also be observed in the flushing of tulips, by which they lose their variegated colors when treated with strong manure. The brightness of the floral hues is also increased by crossing. When a white flower is crossed by a yellow, red, or blue flower, a part of the hybrid offspring contain pigments. When lowland white flowers have been cultivated in the intense light of alpine heights, they have in some species become red. Though the conditions are abnormal a rapid development in size and color in an individual flower may be caused by the sting of a gall-fly; for example, all of the organs of *Cratægus coccinea* become bright red and the change of coloring is accompanied by an increase in size.

[1] Hildebrand, F. *Die Farben der Blüthen*, p. 70.

[2] Henslow, G. *On the Self-Fertilization of Plants*, p. 327.

The appearance of bright coloration is here marked by an increased protoplasmic activity.

This view of the origin of white flowers explains why they are commonest in Nature, accounts for their being most numerous in families in which yellow flowers are likewise numerous, and why they are most true to name under cultivation. We can also understand that such flowers under forcing would be more likely to develop a desired color than one already containing pigments.

Red Flowers.— From its wide distribution among plants red coloring naturally follows yellow and white in flowers. Light which is destructive of chlorophyll stimulates the formation of anthocyan. With the increase of white flowers in size and vitality, accompanied by an increase of the sugar content,[1] they very frequently develop red coloration. In the Rosaceæ and Pomaceæ a series of flowers illustrates every step of the transition from white to red. The species of Rubus and Cratægus are usually white or occasionally red, but *Rubus odoratus* is purple red with a white form. In the familiar genus of Malus the species are tinted or strongly shaded with rose, which in the fragrant flowers of *M. coronaria* becomes the predominant color. In Rosa the species are regularly rose or pink varying in several species to white. Red flowers are derived often from white, sometimes from yellow, and occasionally by reversion from blue. They are the rarest in our flora. There are twenty-two species in the Monocotyledons, forty-five in the Apetalæ, eighty-four in the Polypetalæ, and one hundred and six in the Gamopetalæ. Red flowers occur both in the older and more recently evolved families, while blue flowers are restricted to the latter. Red coloration must be regarded of earlier origin in the sequence of floral colors than blue; and, as has been already pointed out, it is also much more common in the vegetative organs of both the angiosperms and cryptogams. In the following families red and blue and blue-purple flowers are the most common:

[1] It is not unlikely that the higher intensity in color of Alpine flowers is due to an increase of the sugar content, but, according to Overton, in most cases of white-flowered varieties it is probably that some other compound rather than a sugar is wanting.

Families.	Red	Blue.	Purple.	Yellow.	White.	Green.	Total.
Liliaceæ	11	6	1	6	13	1	38
Orchididaceæ . .	8		14	10	18	11	61
Polygonaceæ . .	11		3	5	22	33	74
Caryophyllaceæ .	22		2		56	8	88
Rosaceæ	13		4	39	35	4	95
Papilionaceæ . .	13	24	88	33	39		197
Malvaceæ . . .	13		4	5	4		26
Onagraceæ . . .	10		6	24	14	3	57
Ericaceæ	10		5	22	1		38
Vacciniaceæ . . .	11				10	2	23
Gentianaceæ . .	10	16	4	1	7		38
Polemoniaceæ . .	10	8	3		7		28
Labiatæ	12	33	47	4	24		120
Total . . .	154	87	181	149	250	62	883

It is evident that the families containing red flowers may be separated into two series. In the first, which includes the Polygonaceæ, Caryophyllaceæ, Rosaceæ, Malvaceæ, Onagraceæ, Ericaceæ, and Vacciniaceæ, there are red flowers but no blue. These families are primitive with regular flowers, which are frequently of small size and but little modified. The Orchidaceæ offer an exception in which, however, though there are no blue, there are fourteen purple flowers. In the second series, which includes the Liliaceæ, Papilionaceæ, Gentianaceæ, Polemoniaceæ, and Labiatæ, there are both red and blue flowers, which are highly specialized and often dependent on insects for fertilization. Purple flowers belonging to the first series are chiefly red-purple, while those of the second are blue-purple. The Rosaceæ and Papilionaceæ are "sister families," according to Engler; both contain red flowers but there are no blue flowers in the Rosaceæ though they are numerous in the Papilionaceæ. The distribution of the red and blue coloration is probably to be explained by the strong acidity of the cell sap in the first series, and its more nearly neutral condition in the second, so that a comparatively slight variation in the chemical conditions permits the development of either a red or blue flower. A part of the hybrids obtained by Darwin by crossing the red and blue species of Anagallis were red and a part blue, while others were intermediate in color. The same observer also records having seen

a hyacinth with a truss of flowers perfectly blue on one side and perfectly red on the other. Several of the flowers were also striped longitudinally red and blue.

Anthophæïn. — In most instances the brown colors of flowers are caused by a mixture of chlorophyll or carotin with anthocyan. Among brown flowers containing two pigments are *Calycanthus floridus*, *Veratrum nigrum*, *Aristolochia glauca*, *Anona triloba*, Asarum, *Adonis vernalis*, *Ribes grossularia*, and various species of orchids. But in the black spots and brown markings on the flowers of *Vicia faba* and of some species of Delphinium, Möbius finds an olive brown pigment dissolved in the cell sap.[1] As its chemical reactions and optical properties are sufficiently characteristic to distinguish it from other plant coloring substances he proposes for it the name of anthophæïn. The spots on the wings of *Vicia faba* appear black largely because of the papilla-formed structure of the epidermal cells, which become flatter where the markings are brown. The properties of anthophæïn are very similar to those of phycophæïn, the pigment peculiar to the brown Algae ; but it differs from this substance in that it is dissolved in the cell sap, while phycophaeïn, together with chlorophyll, occurs in chromatophores. It is also less soluble in water. Phycophæïn is characteristic for an entire class of plants, while flowers containing anthophæïn are rare.

Purple Flowers. — There are twenty-two purple flowers in the Monocotyledons, twenty-four in the Apetalæ, one hundred and ninety-three in the Polypetalæ, and one hundred and ninety-eight in the Gamopetalæ. Purple flowers may be divided into green or lurid purple, red purple, and blue purple. In the Melanthaceæ there are two small greenish-purple flowers adapted to Diptera. In Trillium of the Convallariaceæ are four lurid purple flowers visited by flies. In the Aristolochiaceæ which are also adapted to Diptera the calyx is lurid purple. These flowers appear to have been derived directly from the primitive green without passing through an intermediate stage. Greenish-purple flowers also occur in the Polygalaceæ and Asclepiadaceæ. Numerous other families contain a few small purplish flowers, which evidently

[1] Möbius, M. Das Anthophæïn, der braune Blüthenfarbstoff. *Berichte deutschen botan. Gesell.* Bd. xviii, p. 341.

belong to a primitive stage of coloring. There are a few flowers which are yellowish-purple. The petals of *Asimina triloba* are at first greenish-yellow changing to a dull purple. In *Geum rivale* the petals are purplish-orange and the calyx brown-purple. Red-purple flowers belong to a higher stage of coloration. They are common in the Orchidaceæ, Geraniaceæ, Lythraceæ, and Onagraceæ. Blue-purple are the most advanced of all, and are common in the Papilionaceæ, Labiatæ and Scrophulariaceæ, families which contain numerous blue bee flowers, to which they are akin in form and color. Many purple flowers also occur in the Compositæ which are partly discoid and partly radiate. Except in a few species where the color stuff is the rare olive brown anthophæin, brown and brown-purple flowers usually contain more than one pigment.

Blue Flowers. — There are only thirty-four blue flowers in the monocotyledons of the Northern States, which belong chiefly to the Commelinaceæ, Liliaceæ, and the Iridaceæ. In the Apetalæ there are no blue flowers, and the purple flowers in this series are primitive in their stage of coloring. The rarity of blue flowers continues in the Polypetalæ. They are most common in the Ranunculaceæ, Papilionaceæ and Violaceæ. In the more primitive families of the Gamopetalæ belonging to the orders Ericales, Primulales and Ebenales blue flowers are again absent. They belong chiefly to the three orders, Gentianales, Polemoniales and the Campanulales. It is, however, in the Polemoniales that blue and blue purple species reach their maximum. There are many bee flowers greatly modified both in form and color and displaying a high degree of variegation. The culmination of color specialization, as has been previously shown in detail, is reached in this order. It will be observed that blue flowers occur almost exclusively in the most specialized families, or when they are present in a more primitive family, as in the Ranunculaceæ, it is in genera which have been highly modified, as in Delphinium and Aconitum. These families and genera are the most recent in their evolution, and blue is consequently the most recent of the floral colors to be developed. Blue flowers are usually derived from red or white forms, but in several families they appear to have yellow-flowered ancestors. Müller believed

this to be the case in the Violaceæ and in Gentiana and in *Myosotis versicolor*. The sequence of the floral colors has been determined by the properties and distribution of the plant pigments, rather than by the selective influence of insects.

Two Color Series. — The colors of flowers may be divided into two series, a primitive series consisting of green, white and yellow, and a derivative series composed of red, purple and blue. In the first the pigments are insoluble and are contained in plastids or are absent. In the second they are dissolved in the cell sap. Of the 4020 northern angiosperms 3001 belong to the first series, while 1019 belong to the second. Of the 2972 entomophilous species 1968 belong to the first and 1004 to the second series. The flowers of the second series are far more numerous in the Polypetalæ and Gamopetalæ than in the Monocotyledones and Apetalæ. The pigments of the first series are most common in primitive families, where the flowers are rotate and but little modified. Very many flowers of the second series have the petals green, whitish, or yellowish in the bud or at the base. In the color changes which takes place in individual flowers green may be succeeded by every color, and red and blue frequently pass through a white or yellow stage. In individual flowers the tendency of green, white, and yellow to change to red and blue is much stronger than the reverse.

Pigments not Induced by Insects. — The function of forming pigments has not been induced by insects. It is a property possessed by all plants from the lowest to the highest. Not only chlorophyll but carotin and other pigments are widely distributed among the algæ. This function is fully developed even among minute unicellular plant organisms. The chromogenous Bacteria are capable of producing colors of remarkable intensity, as red, rose, yellow, orange, green, blue, violet, and black. Four different pigments, as black, blue, green, and yellow, are produced by the *Bacillus pyocyanus*. The red of *Micrococcus prodigiosus* can be extracted by alcohol, discolored by alkalies and restored by an acid. Intense light and acids in small doses increase the production of the pigments, and the alkalies have the reverse effect.[1] Bohn considers the study of Bacteria as

[1] Bohn, G. *L'Evolution du Pigment*, p. 44.

of much interest from their supposed similarity in origin and composition to the pigment granules. According to this author the chromoplastids have their origin in the nuclear chromatin, and are designed to protect the organism from the chemical and physical variations to which it is exposed. A remarkable difference is exhibited by plants in their capability of forming pigments. The four great divisions of the Algæ are characterized by the presence of a green, blue, brown, or red pigment, which in the last three classes is so abundant as to completely mask the chlorophyll. The Fungi display many brilliant colors, which in the Phalloideæ become ecologically important, and prophetic of their attractive office among the Phænogams. In this family flesh flies are allured by the bright coloring, associated with a sweet substance and a nauseous scent, and aid in disseminating the spores. In their form and vivid colors the Balanophoraceæ show a marked resemblance to Fungi. Many conifers and deciduous shrubs and trees display a bright yellow foliage, from which chlorophyll is absent. There is also a great variety of trees and shrubs and herbaceous plants both in tropical and temperate regions, which possess a red, purple, or variegated foliage, which is highly ornamental. Conversely many pale green species exhibit scarcely a trace of bright coloration. The petals are only modified leaves and their colors are closely correlated with the coloration of the vegetative organs. It is often possible from the inspection of the stem and leaves of a plant to determine the color of the flowers it will produce.

Of no Physiological Significance. — With the exception of chlorophyll the pigments are of no physiological significance in the development of flowers. Their function is wholly ecological, and any other effect they may produce is slight and incidental. Negative evidence of this is furnished by the great number of white flowers. Red and blue coloring frequently does not appear until the flower is on the point of expanding. And even after fertilization or in wilting the colors may brighten or change. Bright coloration in flowers, as in fruits, marks the approach of maturity and decay. According to Massee many of the beautiful colors of fungi are of no obvious use.[1]

[1] Massee, G. *Evolution of Plant Life*, p. 145.

Conspicuousness Due to Insects.— Bright coloring in flowers, usually accompanied by an enlargement of the perianth, has been evolved through the agency of insects. Wind-flowers are small and green or dull colored. "In New Zealand where insects are so strikingly deficient in variety, the flora is almost as strikingly deficient in gaily-colored blossoms." [1] In many genera as the flowers become more conspicuous, there is an increase in the number of visitors and the power of self-fertilization is lost. A colored perianth, which contrasts strongly with the surrounding green foliage, can evidently be more easily seen by both insects and birds. For the same reason a contrast in color between different species in blossom at the same time is advantageous. Insects would be likely to make their visits indiscriminately in a monochromatic Flora, as now happens in the case of similarly colored species of buttercups and goldenrods. In the Alps, where owing to the shortness of the summer all of the species blossom at the same time, there is the greatest variety of colors. It is a well known principle of physics that when a red and yellow card are placed side by side each appears more brilliant than when viewed alone, that is the effect of bringing two colors not complimentary in competition is to move them farther apart.[2] The utility of color contrast is sufficient to explain the evolution of floral colors without recourse to the hypothesis that they afford pleasure to insects.

Insects and Flowers.— The influence of insects upon the evolution of flowers has undoubtedly been greatly overestimated. There is certainly no satisfactory evidence that the ancestors of all angiospermous flowers were once entomophilous, and that the wind-fertilized forms are the result of degeneration. In my opinion not only the principal plant series but many families and genera were developed before the habit of flower visiting became established. The formation of this habit must have required a considerable interval of time. Neither is there sufficient evidence to support the claim that the color of every flower has been determined by the pleasure it afforded to the pollinating insects.

[1] Thompson, George M. Fertilization of New Zealand Flowering Plants, *Trans. Proc. New Zeal. Inst.* 1880. Opinion of A. R. Wallace.

[2] Rood, O. N. *Text-Book of Color*, p. 246.

Some of the adherents of this theory have not, however, hesitated to cause a flower to undergo several changes of color in order that its present hue may conform to their imaginary views of its origin. Further observations are required to determine how far a sense of color is developed among insects, but the writer believes that the colors of flowers have determined the color sense of insects rather than the converse. It is desirable to review briefly the evidence of a preference for certain floral colors in the four orders of insects,—the Coleoptera, Diptera, Lepidoptera, and Hymenoptera,—which are important as flower visitors.

Coleoptera. — There is no evidence that the Coleoptera have exerted any influence on the particular coloration of flowers. They are often poorly adapted for flower visiting, a habit which they have acquired at a comparatively recent date. They probably give the preference to bright colors, but they do not avoid dull yellow or green. None of our northern species are adapted to Coleoptera, but they are very frequent visitors to rotate clustered white flowers like Viburnum. No inference can be drawn from the beautiful markings often displayed by beetles that they take pleasure in the colors of flowers, for the most intelligent of all flower visiting insects, the bees, wear the plainest dress.

Diptera. — The Diptera as fertilizers of flowers are of much greater importance than the Coleoptera. The Syrphidæ have been thought to hover with delight over bright golden yellow flowers; while the carrion flies, it has been asserted, are attracted by a lurid red or purple inflorescence. In number and importance as flower visitors the Syrphidæ, or drone flies, surpass all other Diptera. The light blue *Verónica chamædrys*, the rose pink *V. urticifolia* and the white *Circæa Lutetiana* are adapted to these flies, but they certainly furnish no evidence that their colors have been evolved by their selective influence. Plateau has recently shown that the Syrphidæ poise before many inconspicuous objects as green flowers, closed buds, green fruits, or even the point of the finger, in the same manner as before yellow flowers. Poising upon the wing before a flower must, therefore, be regarded merely as a habit of flight, and not as evidence that pleasure is experienced. It is, however, probable that as

yellow is the color of honey and pollen the more acute insects may from long experience, as in the case of yellow honey-guides, associate this color with the presence of a supply of food. Another group of flowers have nauseous or indoloid odors due to the decomposition of some nitrogenous compound. They are often flesh-colored, blood red, dull dark purple or red, and sometimes they are marked with livid stripes or spots. By some authors they are regarded as resembling putrifying flesh or decaying carcasses. In most instances the resemblance is not very apparent. Malodorous flowers with other colors as yellowish green or white also occur. These flowers are visited by carrion and dung flies belonging to such genera as Musca, Lucilia, Sarcophaga, and Scatophaga, which are believed to find the supposed resemblance to putrid substances attractive. While there is no improbability in this supposition, it is chiefly, if not entirely, the nauseous odors which attract these insects. The lurid coloring may often be explained by peculiarities of the plants in the production of pigments, as in the Balanophoraceæ, where not only the inflorescence but the whole plant is vividly colored. There are also a large number of flowers with strong scented rather than repulsive odors, which are attractive to flies, as *Anethum graveolens* and some Umbelliferæ.

Lepidoptera. — Various birds and mammals, as is well known, become greatly excited when a red object is held before them. Humming-birds and honey-suckers are attracted by fire-red and scarlet colors. Kerner has pointed out that flowers of these colors are more abundant in the Tropics and in South Africa, where these birds are most numerous; while they are rare in Europe where there are no humming-birds. There would seem to be no *a priori* reason why butterflies, as Müller believed, may not be strongly influenced by red coloration. Of eight Alpine butterfly flowers (*Orchis globosa*, *Lilium martagon* and *L. bulbiferum*, *Gymnadenia odoratissima*, *Dianthus superbus*, *D. silvestris*, *D. atroruber* and *Daphne striata*), all were red colored. Other red butterfly flowers are species of Silene, Lychnis and Primula, *Erica carnea*, and species of Asclepias and Monarda. On the other hand three species of Globularia with light blue flowers are adapted to butterflies, "the only instance in the

German and Swiss flora of a blue color being produced by the selective agency of Lepidoptera." That butterflies visit very frequently flowers of a great variety of colors is well known to every observer. Of 1432 visits made by 100 species of Rhopalocera, 44.8% were made to greenish-yellow, yellow and white flowers; and 55.2% to red, violet, and blue flowers.[1] The percentage of visits to wasp and bee flowers was 16.7%, and to lepidopterous flowers 13.8%; but the greatest number of visits was to flowers of the type of the Compositæ which was 43.2%. The percentage of visits to flowers with the honey exposed or not deeply concealed was small. Essentially the same results were reached by the comparison of 2086 visits of 220 Lepidoptera. The above figures show that butterflies are influenced more by the form of the flower than by its color. Red and blue flowers are usually tubular and contain more honey than yellow and white flowers, which are more often rotate and exposed to pillagers of every sort. The flat, capitate inflorescence of the Compositæ is especially well adapted to butterflies. It is also noteworthy that in the families and genera, which contain red-colored butterfly flowers, blue is very rare or wholly absent. The evidence that red floral coloration is a source of pleasure to butterflies cannot be regarded otherwise than unsatisfactory. Nocturnal Lepidoptera are attracted by brightness, as white or yellow and especially a bright light, rather than by hue.

Hymenoptera. — By putting different colored papers over the entrance holes of ground wasps it has been proven that wasps can quickly distinguish between colors.[2] By a series of well-known experiments Lubbock also showed that different colors were readily recognized by the honeybee. Müller as the result of numerous observations came to the conclusion that the honeybee prefers blue, violet, and various shades of purple and red, to white and yellow and avoids scarlet and lurid colors. During the past summer I repeatedly observed the honeybee collecting pollen on the flowers of the scarlet poppy; and am led to believe that, if these flowers contained nectar, the color would not pre-

[1] Müller, H. *Alpenblumen*, p. 523.

[2] Morely, Margaret. *Wasps and their Ways*; Peckham, G. W. and E. G. Some observations on the Special Senses of Wasps, *Proc. Nat. Hist. Soc. Wisc.*, 1887.

vent the frequent visits of bees. Like butterflies bees are greatly influenced by the form of the flower. The long-tongued bees seldom visit butterfly flowers, pollen flowers, and flowers with the honey fully exposed unless it is very abundant. They are most frequently collected on wasp and bee flowers, and on associations of flowers with the nectar deeply placed. The percentage of visits made by the long-tongued bees to yellow and white flowers in Müller's observations was 36.6%, and to red and blue 63.3%; while the percentages of the short-tongued bees were almost exactly the reverse, or 63.8% to yellow and white, and 36.2% to red and blue flowers. This difference seems to be chiefly due to the form of the flowers rather than to their color, as the short-tongued bees are largely excluded from flowers with the honey deeply concealed. The evolution of bee flowers and that of the long-tongued bees has gone on *pari passu*. The progenitors of the bee flowers were presumably regular, and mostly white or yellow; while Apis, Bombus and the allied genera are descended from forms resembling Prosopis. As the perianth gradually became specialized a whole host of pillaging flies and beetles were shut out, and a more abundant supply of honey remained for the rightful visitors. If these partially developed bee flowers displayed red or blue colors, they would be more easily distinguished by the lawful guests from the great mass of blossoms with the honey unprotected. As the result of long experience the more intelligent bees would learn to associate these colors with an ample supply of food and freedom from unwelcome competitors. White and yellow flowers would tend to disappear in these genera. A preference for blue coloration shown by bees at the present time does not, therefore, necessarily imply that blue affords them an æsthetic pleasure; but only that they recognize the signal of flowers adapted to their visits.

Conclusion. — The colors of flowers both in general and particular have been determined by their utility rather than by an æsthetic color sense in insects. Insects distinguish between different colors, but they do not receive greater pleasure from one hue than from another. Any preference they may manifest has arisen from the association of the colors with the presence of food substances. Conspicuousness, or contrast of the inflores-

cence with the foliage, has been induced by insects. It is of advantage to insects since it enables them to find nectariferous flowers quickly, and to plants because it aids in securing cross-fertilization. Many colors are better than one since the flowers are rendered more conspicuous by contrasts with each other as well as with the foliage, and insects are less liable to visit them indiscriminately. The sequence of colors, green, yellow, white, red, purple, and blue depends upon physiological causes. Plants vary greatly in their capability of forming the different kinds of pigments, and the floral colors are correlated with the variability of this function. The primitive colors green, yellow and white have been determined by the nature of the chloroplast and its pigment content; while red, purple and blue have arisen as the result of various chemical and physical conditions.

Bibliography. — In the preparation of these papers constant use has been made of the works of Müller, Knuth, Kerner, and Darwin; of the Manuals of Gray and Chapman; and of the *Illustrated Flora* of Britton and Brown. Bibliographies of the literature dealing with the mutual relations of flowers and insects and with the colors of flowers will be found in Müller's *Fertilization of Flowers*, translated by D'Arcy W. Thompson, and in Knuth's *Handbuch der Blütenbiologie* (2871 titles). References to 772 books and papers on plant pigments are given in Kohl's *Carotin und seine physiologische Bedeutung*. In his paper "Beobachtungen und Versuche über das Auftreten von rothem Zellsaft bei Pflanzen" Overton briefly reviews the literature relating to anthocyan. For the literature on the colors of animals Newbigin's *Color in Nature* may be consulted.

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